

Rod-cone interactions assessed in inferred magnocellular and parvocellular postreceptoral pathways

Hao Sun¹

Visual Sciences Center, University of Chicago, Chicago, IL, USA



Joel Pokorny

Visual Sciences Center, University of Chicago, Chicago, IL, USA



Vivianne C. Smith

Visual Sciences Center, University of Chicago, Chicago, IL, USA



¹Current address:

State University of New York, College of Optometry, New York, NY, USA

Interactions between receptor-isolating rod and long (L)- or middle (M)-wavelength-sensitive cone modulations at 2 Hz and 10 Hz were analyzed in terms of underlying inferred magnocellular (MC) and parvocellular (PC) postreceptoral pathways. Stimuli originated from a colorimeter with 4 primaries in both the center and surround fields. The first experiment employed a phase paradigm in which the thresholds for mixed rod and cone modulations were measured as a function of relative phase. The amplitudes of the rod and cone modulations, equated in threshold units, were varied in tandem. In the second experiment, thresholds for mixed rod and cone modulations were measured as a function of the ratio of the rod and cone modulation amplitudes for 2 fixed phase offsets. Both experiments yielded similar interpretations of rod and L- (or M-) cone interactions. At 1 and 10 troland (td), rod and L- (or M-) cone interactions varied depending on the postreceptoral pathways underlying the detection. When cone thresholds were mediated by the inferred MC pathway, rod and cone thresholds showed almost linear summation. When cone thresholds were mediated by the inferred PC pathway, rod and cone thresholds showed probability summation. Assuming that signals within the same pathway follow linear summation, and signals traveling in different pathways follow probability summation, we concluded that the rod thresholds were mediated by the inferred MC pathway for both the 2-Hz and 10-Hz conditions.

Keywords: rod vision, magnocellular, parvocellular, contrast sensitivity

Introduction

Anatomical and single-unit electrophysiological studies of the primate retina have found that rods and cones do not have separate visual pathways to the brain; rather, they share the pathways with joint inputs to the retinal ganglion cells (Dacheux & Raviola, 1986; Daw, Jensen, & Bunken, 1990; Schneeweis & Schnapf, 1995; Wässle, Yamashita, Greferath, Grünert, & Müller, 1991). There are at least 2 major retinogeniculate pathways: the MC pathway and the PC pathway, corresponding to the anatomical retinal parasol and midget systems. Although anatomical studies suggested the possibility that rods might provide inputs to both magnocellular (MC) and parvocellular (PC) pathways (Grünert, 1997; Grünert & Wässle, 1996), electrophysiological studies found conspicuous rod input to the MC pathway, but only weak or negligible rod input to the PC pathway (Gouras & Link, 1966; Lee, Pokorny,

Smith, Martin, & Valberg, 1990; Lee, Smith, Pokorny, & Kremers, 1997; Purpura, Kaplan, & Shapley, 1988; Virsu, Lee, & Creutzfeldt, 1987; Wiesel & Hubel, 1966). Lee et al (1997) established that rod input was in phase with the center of the ganglion cell's receptive field, consistent with the anatomical evidence (Daw et al., 1990; Wässle et al., 1991). Rod activity was observed in the majority of MC pathway cells at a retinal illuminance of 20 td and in all such cells at 2 td. In comparison, no rod activity was seen in the PC pathway cells at 20 td and in only 60% of cells at 2 td.

Psychophysical studies with human observers have shown rod-cone interactions with a variety of visual tasks, such as color matching and color discrimination (Montag & Boynton, 1987; Smith & Pokorny, 1977; Stabell & Stabell, 1974, 1975, 1976; Trezona, 1970), hue perception (Buck, 1997; Stabell & Stabell, 1979, 1994), increment threshold (Shapiro, Pokorny, & Smith, 1996a; Sharpe,

Fach, Nordby, & Stockman, 1989a), and flicker threshold (Alexander & Fishman, 1984; Coletta & Adams, 1984; Goldberg, Frumkes, & Nygaard, 1983; MacLeod, 1972). Quantitative studies of rod-cone interactions have usually been directed toward measurement of rod-cone threshold summation (Benimoff, Schneider, & Hood, 1982; Buck & Knight, 1994; Drum, 1982; Ikeda & Urakubo, 1969; Kremers & Meierkord, 1999; Naarendorp, Rice, & Sieving, 1996; van den Berg & Spekreijse, 1977). Most of these studies used pulsed stimuli and many did not consider possible differences in the temporal course of rod and cone responses. Another issue is that many studies have used spectrally selective stimuli to favor rods or cones. The choice of chromaticities may bias detection to one or the other postreceptoral pathways. For example, long wavelength test lights are frequently used as stimuli favoring cones. Detection of small, briefly presented long wavelength stimuli may be ascribed to PC pathway (Hood & Finkelstein, 1983). Conversely, detection of a brief achromatic pulse may be attributed to the MC pathway (Pokorny & Smith, 1997). The degree of rod-cone interaction may vary depending on whether rod and cone signals are conveyed in a single pathway or in parallel postreceptoral pathways to the central nervous system. Few psychophysical studies have been directed to the question of rod input to postreceptoral pathways (D'Zmura & Lennie, 1986; Lennie & Fairchild, 1994).

Our goal was to examine psychophysically how rod and cone signals combine for stimulus conditions for which we can infer the postreceptoral pathway that mediates cone threshold and, further, how rod signals might be fed into the postreceptoral pathways. We investigated rod-cone interactions with a 4 primary colorimetric system that allowed independent stimulation of all 4 types of photoreceptors, short (S)-, middle (M)-, and long (L)-wavelength-sensitive cones and the rods (Sun, Pokorny, & Smith, 2001a). With this device, we could also bias detection to one or the other postreceptoral pathways. Cone-isolating stimuli provide input to both the luminance and chromatic postreceptoral pathways. Previous studies (Kelly & van Norren, 1977; Smith, Pokorny, Davis, & Yeh, 1995) inferred that L- and M-cone modulation thresholds were mediated by the chromatic pathway at lower temporal frequencies and by the luminance pathway at higher temporal frequencies. We used 2 Hz and 10 Hz temporal modulation to bias cone detection to the presumed PC or MC pathway.

Methods

Apparatus

The 8-channel colorimeter, described fully by Sun et al (2001a), presented a 6° circular center and a 16° annular surround. The center and the surround each consisted of 4 primary lights, 459 nm, 516 nm, 561 nm, and 664 nm with half-height bandwidths of 8 to 10 nm. The observer viewed the stimulus field through a 2-mm artificial pupil. A fixation point allowed the field to be viewed at 10° in the temporal retina.

Stimuli

In a preliminary set of measurements, we established that each observer's receptor sensitivities at the wavelengths of the colorimeter primaries could be characterized as linear transforms of the 1964 CIE 10° standard observer data, after correcting for prereceptoral filtering differences between the individual and the standard observer (Sun et al., 2001b). Following prereceptoral filtering correction, the rod spectral sensitivity was characterized by the CIE scotopic luminosity function $V'(\lambda)$, and the L, M and S cone spectral sensitivities by the Smith-Pokorny transformation (Smith & Pokorny, 1975) applied to the 1964 10° color-matching functions (Shapiro, Pokorny, & Smith, 1996a). In a previous study of temporal modulation sensitivity (Sun, Pokorny, & Smith, 2001b), we established that the rod- and cone-isolating stimuli appeared uniform in the 6° center and gave temporal contrast sensitivity functions characteristic of the rod, S cone, or L (or M) cone.

A rod modulation, a cone modulation, or a mixture of the 2 modulations was presented in the center. Both the rod and cone modulations were sinusoidal temporal modulations. The cone modulation could be one of the following: L cone, M cone, luminance (L+M), or equiluminant chromatic (L-M) modulation. The modulation frequency was either 2 Hz or 10 Hz. The time-average illuminance of the center was 1 photopic td (0.483 scotopic td) or 10 photopic td (4.83 scotopic td). The time-average chromaticity of the center was metameric to the equal energy spectrum for the 1964 CIE 10° standard observer. The surround was either dark (dark surround) or fixed at the time-average illuminance and chromaticity of the center (equiluminant surround).

Observers

Three observers, H.S. (author), S.G., and S.S., participated in the experiments. S.G. and S.S. were naïve observers. All observers were normal trichromats, as

assessed with the Ishihara pseudoisochromatic plates and the Neitz OT anomaloscope. The Farnsworth-Munsell 100-hue error scores for H.S., S.G., and S.S. were 4, 10, and 20, respectively. H.S. and S.G. were myopic (-5.5, -5.0), and wore nontinted contact lens during experiment. S.S. was emmetropic. Observer H.S. participated in both experiments. Observer S.G. participated in experiment 1 and S.S. participated in experiment 2.

Procedure

Following 30 minutes of dark-adaptation prior to testing, the observer adapted to the time-average center illuminance and chromaticity for 3 minutes. The method of adjustment was used to estimate the thresholds. The mean thresholds and standard deviations were based on 10 trials from 2 sessions (for observers H.S. and S.S.) or 5 sessions (for observer S.G.).

First, the thresholds for rod modulation and the specific type of cone modulation were measured separately. Then the thresholds for mixed rod and cone modulations were measured with the rod and cone modulations varied in tandem. For experiment 1, the contrasts of the 2 modulations were maintained at a constant ratio of 1:1 in threshold units, and the phase offset was varied. For experiment 2, the contrasts of the 2 modulations were varied from 2:1, 1:1, or 1:2 in threshold units, and the phase offset was fixed. For both experiments, the phase offset was expressed as the phase of the cone stimulus relative to the rod stimulus.

Experiment 1. Phase Paradigm

The phase paradigm was previously described by Lindsey, Pokorny & Smith (1986) and Swanson, Pokorny & Smith (1987a, 1988). In the current implementation of the phase paradigm, the rod and cone temporal modulations were always equated in threshold units. Thresholds for the mixed rod and cone modulations were measured at 12 different rod-cone phase offsets (Figure 1A). Phase offset was randomized from trial to trial. If the rod and cone systems were independent, thresholds for the mixed rod and cone modulations would not vary with the relative phases between the 2 modulations. If the rod and cone systems followed complete linear summation within one pathway, thresholds for mixed rod and cone modulations would vary with relative phases between the rod and cone modulations. The threshold would be minimal when the rod and cone responses were in phase, and maximal when the rod and cone responses were out of phase. The phase offsets that corresponded to the minimal

and maximal thresholds might reveal the time delay between the rod and cone responses.

Template fit

The data were fit with 2 templates: a linear-summation template and a probability-summation template. Figure 1A shows model predictions for linear summation and probability summation of the rod and cone modulations. Linear summation would be expected if the rod and cone signals shared a common postreceptoral pathway. Probability summation would be expected if the rod and cone signals traveled in separate pathways to the decision site.

(1) Linear-summation template

A sinusoidally modulated rod stimulus at threshold contrast can be written as

$$C_{rod-threshold} * \sin(2\pi ft + \theta_{rod})$$

where f is the temporal modulation frequency, θ_{rod} is the phase of the rod modulation, and $C_{rod-threshold}$ is threshold contrast of the rod modulation. The response to the rod stimulus A_{rod} at the locus in the visual system where the rod and cone signals combine can be written as

$$A_{rod} = C_{rod-threshold} * \sin(2\pi ft + \theta_{rod} + \Phi_{rod}) / C_{rod-threshold} \quad (1)$$

where Φ_{rod} is the physiological phase of the rod response.

Similarly, a sinusoidally modulated cone stimulus at threshold contrast can be written as

$$C_{cone-threshold} * \sin(2\pi ft + \theta_{cone})$$

where θ_{cone} is the phase of the cone modulation, and $C_{cone-threshold}$ is threshold contrast of the cone modulation. The response to the cone stimulus A_{cone} at the locus in the visual system where the rod and cone signals combine can be written as

$$A_{cone} = C_{cone-threshold} * \sin(2\pi ft + \theta_{cone} + \Phi_{cone}) / C_{cone-threshold} \quad (2)$$

where Φ_{cone} is the physiological phase of the cone response.

In the experiment, the phase of the rod modulation was fixed at 0° , and the phase of the cone modulation θ_{cone} can be replaced by the physical phase offset between rod and cone stimuli $\theta_{rod-cone}$.

If the rod and cone signals travel in the same pathway and are summed linearly, the response $A_{rod+cone}$ to the mixed rod and cone modulations can be written as

$$A_{rod+cone} = \sin(2\pi ft + \Phi_{rod}) + \sin(2\pi ft + \theta_{rod+cone} + \Phi_{cone}) \quad (3)$$

and the threshold ratio of mixed rod and cone modulation to rod modulation alone is determined by the ratio of the response amplitudes

$$C_{rod+cone} / C_{rod} = \max\{\sin(2\pi ft + \Phi_{rod})\} / \max\{\sin(2\pi ft + \Phi_{rod}) + \sin[(2\pi ft + \Phi_{rod}) + (\theta_{rod+cone} + \Phi_{cone} - \Phi_{rod})]\}$$

$$\text{for } 0^\circ < 2\pi ft + \Phi_{rod} < 360^\circ \quad (4)$$

where $\theta_{rod+cone}$ is the independent variable in the template. $\Phi_{rod} - \Phi_{cone}$ represents the physiological phase delay between rod and cone responses, and it is a free parameter that allows the template to shift horizontally. Both the shape and the vertical position of the template are fixed.

(2) Probability-summation template

If rod and cone signals travel in two pathways and are detected independently, their thresholds will follow probability summation. The probability of detecting a mixture of rod and cone modulations $P_{rod+cone}$ is given by

$$P_{rod+cone} = 1 - (1 - P_{rod}) * (1 - P_{cone}) \quad (5)$$

where P_{rod} and P_{cone} are the probability of detecting rod modulation and cone modulation. P_{rod} and P_{cone} represent two points on the psychometric functions of rod and cone modulation, respectively. If rod and cone thresholds show probability summation, the ratio of mixed rod and cone modulation threshold to rod threshold alone $C_{rod+cone} / C_{rod}$ must be smaller than 1. The exact value of the threshold ratio depends upon the slopes of the psychometric functions. If rod and cone signals follow probability summation, the rod and cone phases should have no effect on the threshold.

We can fit the data with a straight line

$$C_{rod+cone} / C_{rod} = a \quad (6)$$

where a is a free vertical scaling factor.

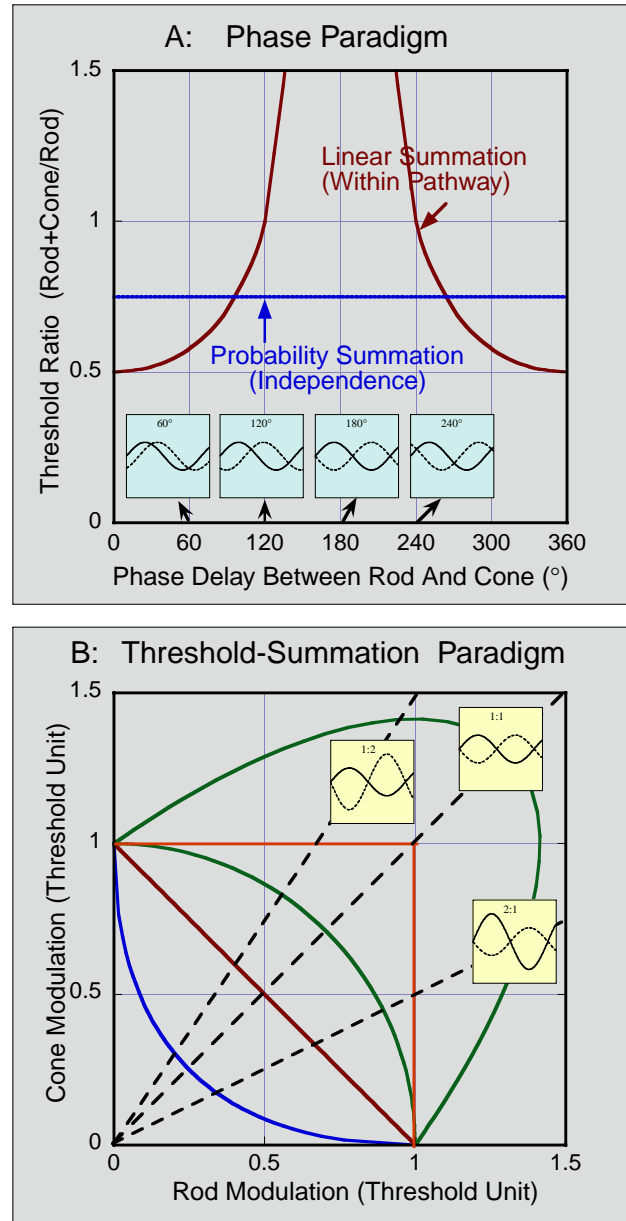


Figure 1. Schematic diagram describing the phase paradigm (A), and the threshold-summation paradigm (B). In the phase paradigm, the rod and cone modulations were maintained at a constant ratio of 1:1 in threshold units, and contrast thresholds for mixed rod and cone modulations were measured as a function of the phase offsets between rod and cone modulations. In the threshold-summation paradigm, the phase offset of the rod and cone modulation was kept constant, and contrast thresholds for mixed rod and cone modulations were measured as a function of the ratio of the rod and cone modulation amplitudes.

Results

In a set of initial measurements, we assessed the contrast thresholds for the rods and the L and M cones in isolation, as well as contrast thresholds for luminance and chromatic modulations. These measurements were

performed at 2 and 10 Hz at an average retinal illuminance of 1 and 10 td with a time-average chromaticity metameric to equal energy white. The medians of these threshold settings are shown in Table 1. Thresholds for S.G. were uniformly higher than for H.S. S.G. could not make isolated L and M cone settings at 10 Hz and 1 td. Neither observer could make a chromatic setting within the available contrast gamut at 10 Hz and 1 td.

First, we compared the luminance and chromatic conditions. At 2 Hz, chromatic contrast thresholds were lower than luminance contrast thresholds for both observers. The result reverses at 10 Hz where luminance contrast thresholds were lower than chromatic contrast thresholds. These data were consistent with others in the literature (Kelly & van Norren, 1977; Lindsey et al., 1986; Smith et al., 1995; Swanson, Ueno, Smith, & Pokorny, 1987b). The isolated cone thresholds were slightly higher

but closer to the chromatic contrast thresholds at 2 Hz. They were slightly higher but closer to the luminance contrast thresholds at 10 Hz. The data have been interpreted to indicate that the isolated cone sensitivities are processed by different postreceptoral pathways at different temporal frequencies. Our data and interpretation are consistent with previous studies (Kelly & van Norren, 1977; Smith et al., 1995). Within the present context, our data indicated that at 2 Hz, cone thresholds were processed in chromatic pathways, and at 10 Hz, cone thresholds were processed in achromatic pathways. We thus expect that the combined modulation of cones and rods will reveal interactions between the pathway that mediates cone detection at the specific temporal frequency and the more sensitive pathway that carries the rod signals at that frequency.

Table 1. Modulation thresholds for L cone, M cone, luminance, chromatic, and rod modulations at different retinal illuminance levels and frequencies.

Subject	Frequency (Hz)	Retinal Illuminance (td)	Threshold Contrast (%)				
			L cone	M cone	Luminance	Chromatic	Rod
H.S.	2	1	3.19	3.37	9.77	2.59*	7.61
	2	10	1.69	2.05	2.75	1.09*	7.65
	10	1	15.23	16.05	12.12*		6.05
	10	10	2.20	5.69	2.09*	10.17	3.83
S.G.	2	1	7.18	7.68	11.37	5.69*	10.20
	2	10	2.16	2.85	3.67	2.47*	6.64
	10	1			17.12*		10.85
	10	10	5.92	4.92	3.80*	7.80	5.57

* Indicates the more sensitive pathway.

In the main experiment, rod and cone thresholds were checked at the beginning of each experimental session to make sure that they were close to the contrast threshold values of Table 1. The rod and cone contrasts were then modulated in tandem to obtain thresholds as a function of the phase between the 2 sinusoids. There were no consistent differences between the results obtained with a dark surround and with an equiluminant surround. The dark surround data are shown in the figures. Results for combined rod and L- (or M-) cone modulation, with a dark

surround, at 1 td (0.483 scotopic) and 10 td are shown in Figures 2 and 3, respectively.

To evaluate the data, we first determined if the data could be described by probability summation (Equation 6). We used an F-test to test the null hypothesis that probability summation could describe each data set. We compared the variance contributed by deviations of each phase mean from the grand mean with the variance contributed by deviations of each repetition at a given phase from its phase mean. The majority of data sets at 2

Hz were consistent with probability summation. Moderately high F ratios in the 2-Hz data occurred for the M cone isolation condition, but the variation among the phase means occurred at random phase angles. Probability summation was rejected for the 10-Hz condition at $P_F < .01$, except for the 10-td, L-cone condition for S.G. where $P_F < .05$. We, therefore, show the probability summation fits for the 2-Hz data and linear summation fits for the 10-Hz data.

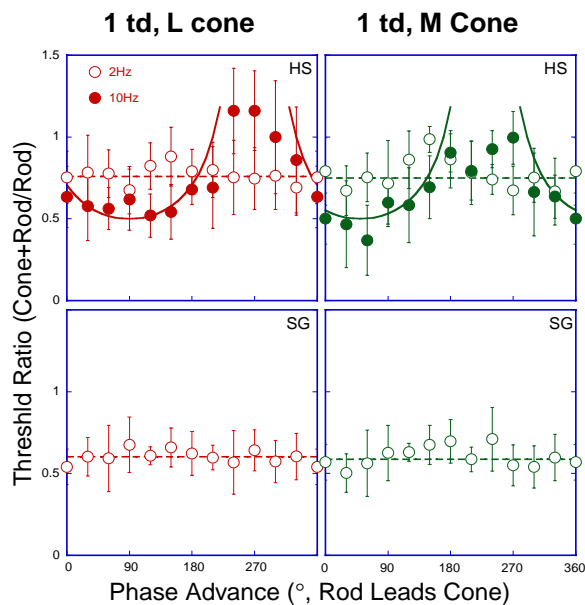


Figure 2. Thresholds for combined rod with L- (or M-) cone modulation at 1 td with a dark surround. The 2 upper panels show data for observer H.S. The 2 lower panels show data for observer S.G. For both observers, the left panels show rod and L-cone data, and the right panels show rod and M-cone data. Data are shown for 2 frequencies: 2 Hz (open symbol) and 10 Hz (solid symbol).

In summary, the pattern of thresholds for mixed cone and rod modulation depended on the modulation frequency. At 2 Hz, the threshold contrasts showed little variation with relative phase, and were consistent with the probability summation model. At 10 Hz, the threshold contrasts for observer H.S. showed clear variation with phase with a maximum near 210° , and were consistent with the linear summation model. A similar trend was noted for S.G. Data for observer S.G. showed a smaller effect of phase variation at 10 td, and, of course, no data were obtained for her at 1 td.

Results for combined rod with luminance or chromatic modulation at 10 td with a dark surround are shown in Figure 4. Again, we first determined if the data could be described by probability summation (Equation 6). Here a different result emerged. Probability summation proved an

adequate fit for chromatic and rod modulation at both 2 and 10 Hz for both observers. The probability summation fits are shown in Figure 4 (right panels). Probability summation was rejected for luminance modulation for H.S. at both 2 and 10 Hz ($P_F < .01$) and for S.G. at 10 Hz ($P_F < .05$). The linear summation fits are shown for luminance and rod modulation at both 2 Hz and 10 Hz. For the luminance data at 2 Hz for S.G., probability summation could not be rejected ($P_F < .10$), but the trends of the data were similar to those seen for H.S.

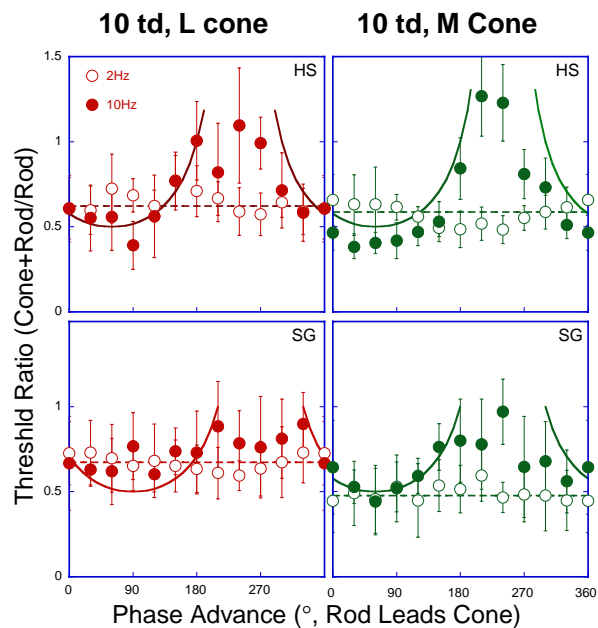


Figure 3. Thresholds for combined rod with L- (or M-) cone modulation at 10 td with a dark surround. The format is the same as for Figure 2.

Interpretation

Based on our threshold data and previous literature studies (Kelly & van Norren, 1977; Lee et al., 1990; Smith et al., 1995), we inferred that isolated L- and M-cone modulation was processed by the PC pathway at 2 Hz and by the MC pathway at 10 Hz. The phase data for isolated cone and rod modulation yielded a clear dichotomy, depending on temporal frequency. At 2 Hz, where the isolated cone thresholds were inferred to be mediated within a chromatic PC pathway, we observed probability summation. At 10 Hz, where the isolated cone thresholds were inferred to be mediated within an achromatic MC pathway, we observed linear summation. These findings were further substantiated by the data using chromatic and luminance modulation to isolate the inferred pathway. In this case, it was the modulation type not the temporal frequency that determined the rod-cone interaction.

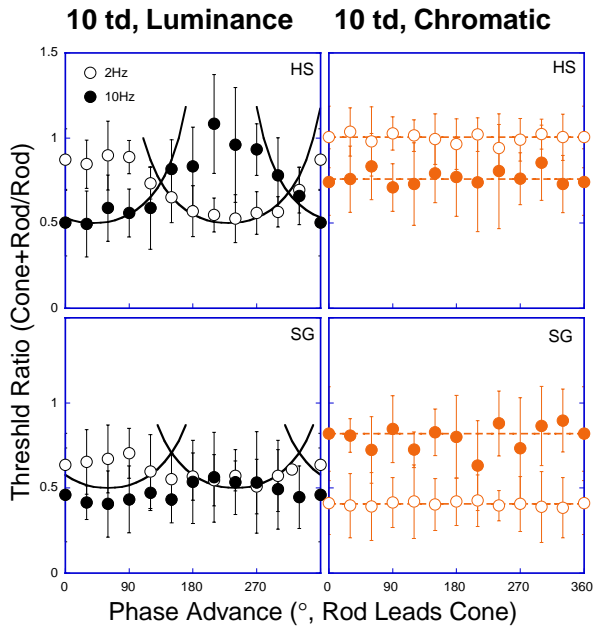


Figure 4. Thresholds for combined rod with luminance, or chromatic modulation at 10 td with a dark surround. The format is the same as for Figure 2.

With chromatic modulation in the inferred PC pathway, we observed probability summation at both 2 and 10 Hz. With luminance modulation in the inferred MC pathway, we observed linear summation at both 2 and 10 Hz. If we assume that signals within the same pathway follow linear summation, and signals traveling in different pathways follow probability summation, we conclude that the rod thresholds were mediated by the inferred MC-pathway for both the 2-Hz and 10-Hz conditions. This conclusion is consistent with the single-unit electrophysiological studies reviewed in the "Introduction" that found more conspicuous rod activity in MC-pathway cells at the retinal illuminances we used (1-10 td).

The linear summation model (Figure 1A) predicts infinite threshold when rod and cone responses are 180° out of phase. There are at least 3 possible reasons that we did not find complete cancellation (Figures 2-4). (1) Psychophysical thresholds probably represent summing of signals from many cells. Cell data show intrinsic variation in temporal properties (Lee et al., 1990), and the summed response, thus, has residual activity at the phases of maximal cancellation of individual units. (2) Differing temporal responses of the rod and cone systems could lead to incomplete cancellation between the rod and cone responses. (3) If the rod signal travels predominately in the MC pathway, and the cones produce responses in both the MC and PC pathways, then the cone signals in the PC pathway could mediate thresholds when rod and cone responses were out of phase in the MC pathway.

Experiment 2. Threshold-Summation Paradigm

We interpret experiment 1 as showing that rod stimulation was processed in the MC pathway. The data were unambiguous for observer H.S., but the conclusion was less robust for observer S.G. Therefore, we decided to extend the paradigm using a quantitative evaluation of summation. In experiment 2, we used a threshold-summation paradigm at 10 td and collected data for observer H.S. and a new observer, S.S. In the threshold-summation paradigm, the phase offset was kept constant, and thresholds for mixed rod and cone modulations were measured as a function of the rod and cone modulation ratio (Figure 1B). For example, rod and cone modulations could be 1:1, 1:2, or 2:1 in threshold units. Stimuli were presented at 1 of the 2 phases that gave the peak and trough thresholds in the corresponding stimulus condition in experiment 1. For 10 Hz, 30° and 210° phase offsets were selected for observer H.S., and 60° and 240° phase offsets were selected for observer S.S. For 2 Hz, the threshold function from the phase paradigm was flat, and no clear peak or trough could be found. The choice of phase was not critical. We used the same phase offsets as those of the 10-Hz condition. The illuminance and chromaticity of the surround were set at the time-average illuminance and chromaticity of the center.

Each experimental session included 5 rod and cone modulation ratios (2:1, 1:1, 1:2, rod alone, and cone alone), and 2 phase offsets at each rod and cone modulation ratio. The rod-cone modulation ratios and the phase offsets were randomized from trial to trial.

Model Fits

The data were fitted with 2 models: the vector-summation model and the Quick pooling model (Quick, 1974). The 2 models could capture data in different regions of the threshold-summation plot. The vector-summation model could fit data showing linear addition, probability summation, or cancellation, but could not fit data showing a peak-detection mechanism. The Quick pooling model could fit data showing linear addition, probability summation, or peak-detection mechanism, but could not fit data showing cancellation. Therefore, for data showing cancellation, only the vector-summation model was used.

Vector-summation model:

$$A = \{x^2 + y^2 + 2 * x * y * \cos(a)\}^{1/2} \quad (7)$$

Quick pooling model:

$$A = (x^k + y^k)^{1/k} \quad (8)$$

where x and y represent the responses to a rod modulation and a cone modulation, respectively, and A represents the response to the mixed rod and cone modulations. a and k are the free parameters in the models, and they indicate the strength of summation between rod and cone modulations.

Results

The summation plots for mixed rod with L- (or M-) cone modulation at 2 Hz are shown in Figures 5 and 6 and at 10 Hz in Figures 7 and 8. Table 2 gives the summation angle a for the best vector-summation model fits and exponential k for the best Quick pooling model fits for all experimental conditions.

At 2 Hz, thresholds for rod and L- (or M-) cone modulation showed the characteristic shape of probability summation at both phase offsets. The 2 models gave equivalent fits. The values of the exponent k in the Quick formula varied from 1.54 to 3.27 among conditions and observers without any systematic trends. The corresponding values of angle a in the vector summation formula varied from 79° to 105°.

At 10 Hz, thresholds for rod and L- (or M-) cone modulation showed close to linear addition for the in-phase condition, and cancellation for the out-of-phase condition. Observer S.S.'s M cone threshold could not be measured at 10 Hz within the contrast range of the colorimeter. The fits for the in-phase data were equivalent for the 2 models. The values of the exponent k in the Quick formula are from 0.91 to 1.41 for observer H.S. and 0.94 for observer S.S. The corresponding values of angle a in the vector-summation model varied from 0° to 72°. The Quick model could not fit the cancellation data. The values of a in the vector-summation model ranged from 122° to 149°.

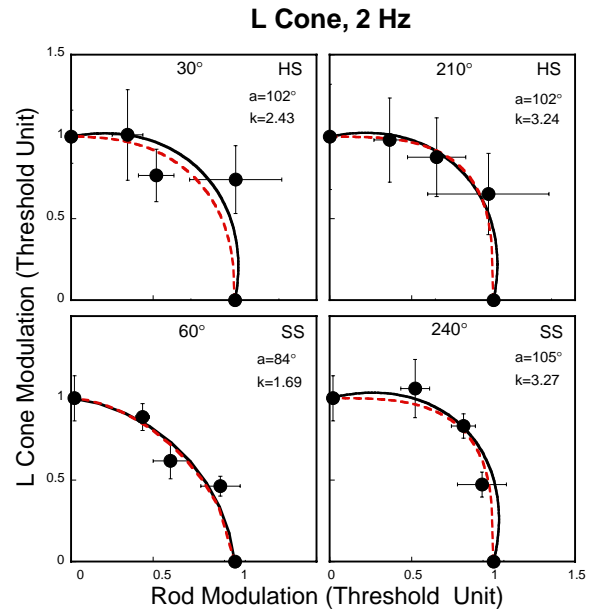


Figure 5. Summation plots for rod and L-cone modulation at 10 td, 2 Hz, and 2 phase offsets. The 2 upper panels show data for observer H.S. at 30° and 210° phase offsets. The 2 lower panels show data for observer S.S. at 60° and 240° phase offsets. The symbols represent experimental data; solid lines represent vector-summation fits, and dashed lines represent Quick pooling fits. a and k indicate the summation angle for the vector-summation model fits and the exponential for the Quick pooling model fits. The error bars represent ± 1 SD of the rod and cone modulation component.

Interpretation

The results of the threshold-summation paradigm were consistent with the results of the phase paradigm: rod and L- (or M-) cone interactions varied depending upon the inferred postreceptoral pathways. At 2 Hz, with the cone threshold mediated by the inferred PC-pathway, the rods and L (or M) cones showed probability summation. Variation in the phase offset did not affect the summation between rods and L (or M) cones. At 10 Hz, with the cone threshold mediated by the inferred MC pathway, the rods

Table 2. Parameters for vector-summation model fits and Quick pooling models fits

Rod +	Retinal Illuminance (td)	Frequency (Hz)	Phase (°)	Vector-summation $a(^{\circ})$		Quick pooling k	
				HS	SS	HS	SS
L Cone	10	2	30°/60°	102	84	2.43	1.69
			210°/240°	102	105	3.24	3.27
		10	30°/60°	0	0	0.91	0.94
			210°/240°	127	149		
M cone	10	2	30°/60°	79	95	1.54	2.02
			210°/240°	98	90	2.43	2.02
		10	30°	72		1.41	
			210°	122			

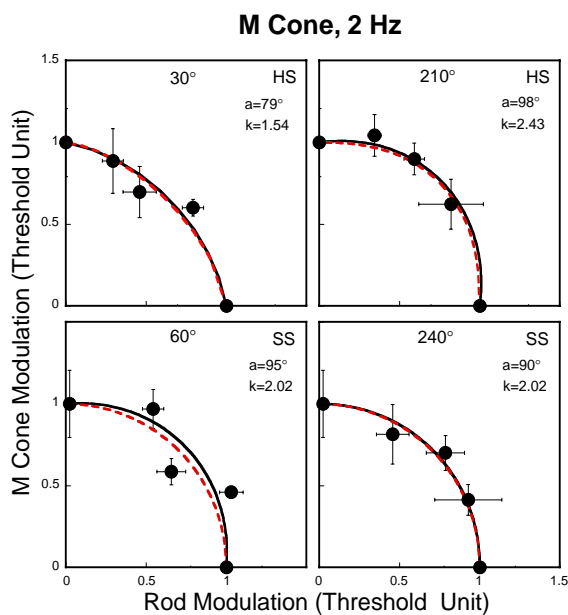


Figure 6. Summation plots for rod and M-cone modulation at 10 td, 2 Hz, and 2 phase offsets. The format is the same as for Figure 5.

and L (or M) cones showed either addition or cancellation depending upon the phase offset. Assuming that signals within the same pathway follow linear summation, and signals traveling in different pathways follow probability summation, we concluded that the rod thresholds were mediated by the inferred MC pathway for the stimulus conditions of these experiments.

Discussion

Psychophysical studies have demonstrated an abrupt transition in the properties of rod vision near 1 scotopic troland. This phenomenon has been hypothesized to represent a change from a "slow" to a "fast" rod pathway (Conner, 1982; Conner & MacLeod, 1977; Sharpe & Stockman, 1999; Sharpe, Stockman, & MacLeod, 1989b; Stockman, Sharpe, Ruther, & Nordby, 1995; Stockman, Sharpe, Zrenner, & Nordby, 1991). The physiological and anatomical basis of two rod pathways is thought to lie in the two different anatomical pathways to ganglion cells, the slow signal via rod bipolar cells and A2 amacrine cells

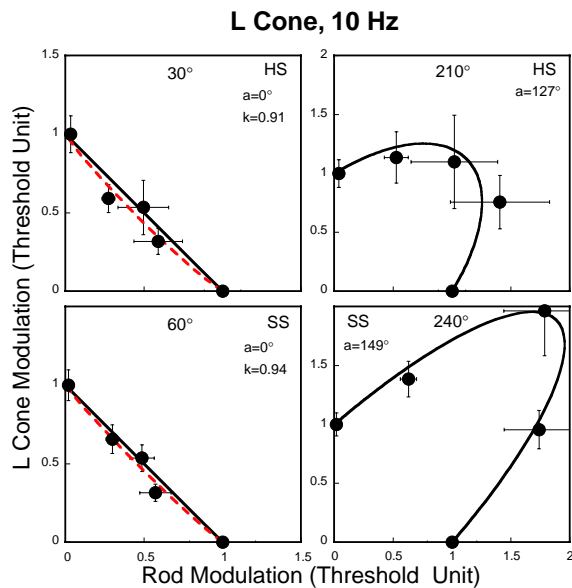


Figure 7. Summation plots for rod and L-cone modulation at 10 td, 10 Hz, and 2 phase offsets. The format is the same as for Figure 5.

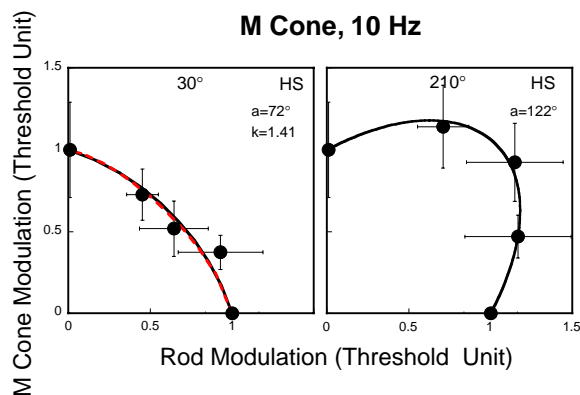


Figure 8. Summation plots for rod and M-cone modulation at 10 td, 10 Hz, and 2 phase offsets. The format is the same as for Figure 5.

through synaptic connections, and the fast signal via cone bipolar cells through rod-cone gap junctions (Dacheux & Raviola, 1986; Wässle et al., 1991). Electrophysiological studies in primate retina have shown a rod response in recordings of the inner segments of isolated cones (Schneeweis & Schnapf, 1999). A rod response can also be recorded in the H1 horizontal cell of the primate (Verweij, Peterson, Dacey, & Buck, 1999). This response had the expected properties of the “fast” rod signal.

Our data, collected near the transition at 0.5 and 4.8 scotopic td, may reflect the properties of either or both rod pathways. The 8- to 20-msec rod-cone delay implied by the phase measurements at 10 Hz suggests predominance of a

fast rod signal, because the slow rod-cone delay is on the order of 75 to 80 msec (Sharpe et al., 1989b; van den Berg & Spekreijse, 1977; Veringa & Roelofs, 1966). The fast rod signal, presumably mediated by gap junctions between rods and cones, shows a latency to peak response time similar to that of cones (Verweij et al., 1999).

The rod-cone gap junction origin of the “fast” rod signal implies rod input would be expected in all cone pathways. What is the origin of the absence of a parvocellular rod signal, both in the single cell and psychophysical measurements? One possibility is that the rod signals in the parvocellular pathway are cancelled because the rod signals would be feeding into both M and L cones and will oppose each other. This idea is not consistent with measurements of PC-cell responses with drifting sine wave gratings chosen to isolate the receptive field center mechanism (Enroth-Cugell & Robson, 1966). Such recordings reveal low responsivity (Purpura et al., 1988; Purpura, Tranchina, Kaplan, & Shapley, 1990), suggesting that low contrast gain may be responsible for the insensitivity of the PC pathway to rod stimulation at mesopic levels.

Conclusions

At 1 and 10 td, rod- and L- (or M-) cone interactions vary depending on the postreceptoral pathways underlying the detection. Rod thresholds are inferred to be mediated by the MC pathway. When L- (or M-) cone threshold is mediated by the inferred MC pathway, rod and L- (or M-) cone thresholds show almost linear summation. When L- (or M-) cone threshold is mediated by the inferred PC pathway, rod and L- (or M-) cone thresholds show probability summation.

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